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# *HARMONIA GUGGOLZIORUM* (COMPOSITAE-MADIINAE), A NEW TARWEED FROM ULTRAMAFICS OF SOUTHERN MENDOCINO COUNTY, CALIFORNIA

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Abstract

*Harmonia guggolziorum* is a new tarweed from ultramafic (serpentine) soils of southern Mendocino County, California. Unlike other species of *Harmonia, H. guggolziorum* combines the following morphological characteristics: primary stems usually longer than branches of the subumbelliform capitulescences, leaves unevenly distributed but not densely congested, heads erect in bud and fruit, phyllaries irregularly hirsute, disc florets bisexual, ray cypselae weakly arcuate, ray pappi present, and disc pappi of linear, fimbriate scales 0.6–0.8 mm long. Based on molecular phylogenetic data, I suggest that *H. guggolziorum* is the only known representative of a lineage that predates diversification of the other serpentine endemic species of *Harmonia* (i.e., *H. doris-nilesiae, H. hallii,* and *H. stebbinsii*). The apparent phylogenetic relationships and geographic location of *H. guggolziorum* lead me to hypothesize that *Harmonia* originated in the southern North Coast Ranges and has undergone more extensive diversification on ultramafics than previously suspected for the genus or any other lineage in Madiinae.

California's exceptionally rich serpentine flora is especially well represented in the northwestern part of the state (Kruckeberg 1984, Harrison et al. 2000), where botanical exploration has continued to reveal previously unknown ultramafic endemics. In the tarweed genus *Harmonia* B. G. Baldwin [=*Madia* Molina sensu Keck (1959) pro parte (i.e., the yellow-anthered, pappose annuals, with $2n = 9$ II); see Baldwin (1999)], two ultramafic endemics (*H. doris-nilesiae* and *H. stebbinsii*) have been described from the North Coast Ranges of California since 1980 (Nelson and Nelson 1980, 1985). Herein, I describe yet another species of *Harmonia* from the North Coast Ranges.

**Harmonia guggolziorum** B. G. Baldwin, sp. nov. (Fig. 1)—TYPE: USA, California, Mendocino Co., on serpentine on the north side of Feliz Creek Road (County Road 109), 2.1 miles west of Hopland (T13N, R12W, S23, NW1/4 of NE1/4), ca. 150–200 plants associated with *Platystemon californicus, Gilia capitata,* and *Cryptantha clevelandii*, 164 m, 30 April 2000, *Jack and Betty Guggolz 1635* (holotype, JEPS; isotype, CAS).

Ab species ceteris Harmoniae characteribus combinatis differt caulibus primariis plerumque ramis subumbelliformium capitulescentiarum longioribus; foliis distributis impariter, non dense congestis, plerumque proximalibus in caulibus primariis et ad basibus capitulescentiarum; capitulis plerumque erectis ante, per, et post anthesin; phyllariis irregulariter et saepe sparsim hirsutis cum pilis prope margines mollibus saepe implicitis; flosculis discorum bisexualibus; cypselis radiorum leniter arcuatis; squamis papporum radiorum fimbriatis, ca. 0.5 mm longis; squamis papporum discorum linearibus fimbriatis ca. 0.6–0.8 mm longis.

*Annual herbs. Stems* erect, branched mostly in distal half, slender, mostly reddish-purple, to 3 dm high, sparsely to densely hirsute proximally, densely stipitate-glandular distally, the glands dark-purplish (or yellowish). *Leaves* opposite proximally, alternate distally, sessile, mostly cauline, unevenly distributed, mostly proximal on primary stems and at bases of capitulescence branches (otherwise sparse or absent), ascending or usually widely spreading, often with reflexed apices; blades linear to filiform, 5–50 mm long (mostly 20–25 mm long on primary stems), 1–3 mm wide, entire or sparsely and shallowly toothed, slightly revolute, hirsute, eglandular or (mostly in capitulescence) stipitate-glandular (especially near apices), the glands dark-purplish (or yellowish). *Capitulescences* subumbelliform, branches often 5–7 cm long (max. 15 cm long) and overtopping the nearly sessile head of the primary stem. *Peduncles* 2–12 mm long, stipitate-glandular, the glands dark-purplish (or yellowish). *Heads* usually erect in bud, anthesis, and fruit. *Involucres* obovoid, ca. 3–4 mm diam. (4–5 mm diam. in pressed specimens). *Phyllaries* (3–) 5 (–6) (1 per ray floret), uniseriate, herbaceous, linear, 4–5 mm long, each completely enveloping a ray ovary, the free apices purplish, erect or spreading, flat or involute, $<1/5$ the length of enfolded basal portion of phyllaries; abaxial faces irregularly and often sparsely hirsute with broadly arching or somewhat appressed hairs, often with soft, matted hairs near margins, ciliate, irregularly stipitate-glandular, the glands dark-purplish (or yellowish). *Ray florets*

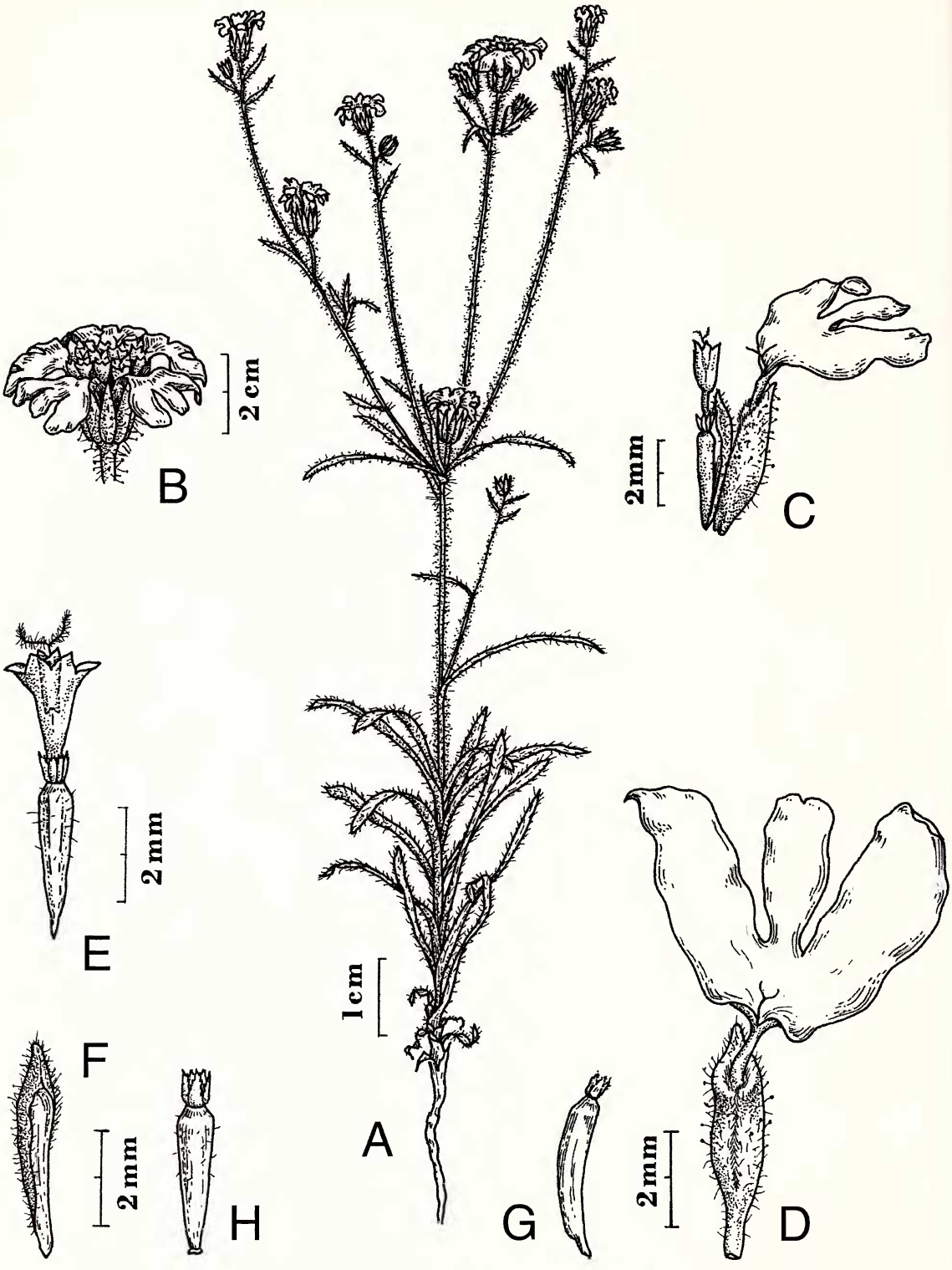


FIG. 1. *Harmonia guggolziorum.* (A) habit; (B) head; (C) phyllary, ray floret, palea, and disc floret (right to left); (D) adaxial view of ray floret and associated phyllary; (E) disc floret; (F) palea; (G) ray cypsela and pappus; (H) disc cypsela and pappus.

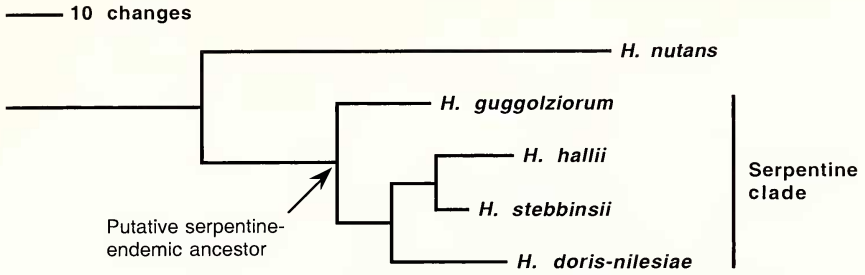


FIG. 2. Relationships in *Harmonia* based on 18S/26S nuclear ribosomal DNA sequences of the external and internal transcribed spacer regions (Baldwin, unpublished). The tree is rooted with sequences from the other diploid members of the "Madia" lineage (Baldwin 1996).

(3–) 5 (–6), pistillate, corollas bright yellow, tubes ca. 1.5 mm long, sparsely hirtellous, laminae broadly overlapping in head, flabelliform, 4–5 mm long, 5–7 mm wide, 3-lobed to ca. half length, glabrous. *Disc florets* 8–13, bisexual, corollas bright yellow, 2–3.5 mm long, tubes much shorter than the narrowly funnelform throats, lobes 5, glabrous abaxially, densely bristly adaxially. *Anthers* yellow. *Style branches* acuminate, hispidulous. *Receptacles* flat, glabrous. *Paleae* not persistent, ca. 8, in one peripheral series, linear, 4–5 mm long, herbaceous near apices or throughout, sometimes chartaceous proximally (especially along margins), flat or with margins partially enveloping a disc ovary, sparsely hirsute and densely ciliate near apices, sparsely stipitate-glandular near apices, the glands dark-purplish (or yellowish), the margins of adjacent bracts free or weakly fused proximally. *Ray cypselae* black, slightly laterally compressed, abaxially rounded, adaxially angled, clavate, weakly arcuate, ca. 3–3.5 mm long, glabrous, beakless. *Ray pappi* of ca. 10–12 stramineous, linear, fimbriate scales ca. 0.5 mm long. *Disc cypselae* black, ±terete to clavate, straight or weakly arcuate, ca. 3–3.5 mm long, with antrorse hairs. *Disc pappi* of ca. 9–11, stramineous or purplish, linear, ±flat (not crisped), fimbriate scales, 0.6–0.8 mm long. *Chromosome number* $2n = 9$ II [reported here from *B. G. Baldwin 1140* (JEPS)].

*Paratype.* USA, California, Mendocino County, on serpentine hillside at junction of Feliz Creek Road (County Road 109) and County Road 110, west of Hopland, 8 May 2001, *B. G. Baldwin 1140* (JEPS).

## KEY TO SPECIES OF *HARMONIA*

1. Heads usually reflexed in bud and fruit; ray pappi 0; disc pappus elements lance-attenuate, fimbrillate, 2–3.7 mm long . . . . . *H. nutans* (Greene) B. G. Baldwin
1′ Heads usually erect in bud and fruit; ray pappi present (often rudimentary); disc pappus elements subulate, linear, oblong, or quadrate, fimbriate or pulmose, 0.2–3.5 mm long.
2. Leaves ± evenly distributed along stems; ray cypselae gibbous (bowed out abaxially), distinctly beaked (beaks <1 mm long); disc florets functionally staminate . . . . . *H. doris-nilesiae* (T. W. Nelson & J. P. Nelson) B. G. Baldwin
2′ Leaves unevenly distributed, mostly restricted to proximal stems and bases of subumbelliform capitulescences; ray cypselae weakly arcuate, beakless; at least some disc florets bisexual.
3. Phyllaries pilose near margins; disc pappus elements subulate, 1.2–3.5 mm long, plumose . . . . . *H. stebbinsii* (T. W. Nelson & J. P. Nelson) B. G. Baldwin
3′ Phyllaries with inconspicuous, soft, often matted hairs near margins; disc pappus elements linear, oblong, or quadrate, 0.2–0.8 mm long, fimbriate.
4. Primary stems usually shorter than branches of the subumbelliform capitulescences; distal leaves of primary stem densely congested; disc pappus elements oblong or quadrate, 0.2–0.5 mm long. . . . . *H. hallii* (D. D. Keck) B. G. Baldwin
4′ Primary stems usually longer than branches of the subumbelliform capitulescences; distal leaves of primary stem not densely congested; disc pappus elements linear, 0.6–0.8 mm long . . . . *H. guggolziorum* B. G. Baldwin

*Relationships.* Based on phylogenetic analyses of 18S/26S nuclear ribosomal DNA sequences of the external and internal transcribed spacers (Baldwin, unpublished), *H. guggolziorum* represents a basally divergent lineage in a monophyletic group comprising all serpentine endemics in *Harmonia* (Fig. 2). Origin of the lineage represented by *H. guggolziorum* apparently predates divergence of *H. doris-nilesiae, H. hallii,* and *H. stebbinsii* from a common ancestor; *H. guggolziorum* is the sister group of the lineage corresponding to *H. doris-nilesiae, H. hallii,* and *H. stebbinsii.* Support for the hypothesis that *H. guggolziorum* represents an ancient, divergent lineage in *Harmonia* rather than a recent product of hybridization comes from unique character-states at eight rDNA nucleotide sites in *H. guggolziorum*

and from four rDNA mutations shared by the other three serpentine species of *Harmonia* but not by *H. guggolziorum, H. nutans,* or any other diploid species of the "Madia" lineage (i.e., diploid species of *Anisocarpus* Nutt., *Carlquistia* B. G. Baldwin, *Jensia* B. G. Baldwin, *Kyhosia* B. G. Baldwin, or *Madia* Molina; see Baldwin 1996, 1999).

*Biogeographic and evolutionary history of* Harmonia. Discovery of *H. guggolziorum* has allowed for refined perspectives on the history of edaphic endemism and overall pattern of diversification in *Harmonia.* Based on phylogenetic analyses of rDNA sequence data (Fig. 2, Baldwin unpublished), the four species of ultramafic endemics in *Harmonia* (*H. doris-nilesiae, H. guggolziorum, H. hallii,* and *H. stebbinsii*) represent a well-supported monophyletic group that is sister to *H. nutans,* an endemic of volcanic-ash exposures in Napa and Sonoma counties, California. In light of the phylogenetic data, I propose a simple hypothesis to explain patterns of edaphic endemism in *Harmonia*: divergence of the ultramafic and volcanic-ash lineages from a common ancestor preadapted (preapted) to "harsh" edaphic conditions, followed by extensive diversification on serpentines in the ultramafic lineage, that is, descent of *H. doris-nilesiae, H. guggolziorum, H. hallii,* and *H. stebbinsii* from a common, ultramafic-endemic ancestor. Lack of diversity in the volcanic-ash lineage may be attributable in part to the limited geographic distribution of volcanic exposures in northwestern California compared to the wide distribution of serpentine exposures in the region (Kruckeberg 1984; Fox et al. 1985).

Phylogeographic considerations lead me to suggest a general history for *Harmonia* of wide dispersal and allopatric diversification among edaphic "islands" (see Raven 1964; Kruckeberg 1991). *Harmonia guggolziorum* and *H. nutans,* represented by two lineages that diverge in succession at the base of the *Harmonia* rDNA tree (Fig. 2), and *H. hallii* are allopatric or parapatric taxa that are endemic or largely restricted to the southern North Coast Ranges (*H. nutans* extends south into the northern San Francisco Bay area). The two species of the northern North Coast Ranges and southern Klamath Ranges (*H. doris-nilesiae* and *H. stebbinsii*) are apically nested in the rDNA tree among the southern North Coast Range lineages and therefore are suggested to be products of dispersal from the south. Based on the rDNA tree topology, *H. doris-nilesiae* and *H. stebbinsii* are not sister species and may represent independent south-to-north dispersal events. Alternatively, the two species may have descended from the same northerly-dispersed ancestor, with *H. hallii* representing an instance of north-to-south dispersal. *Harmonia doris-nilesiae* and *H. stebbinsii* are highly divergent in morphology and molecular sequences and are to my knowledge the only taxa in *Harmonia* that provide an example of sympatry [*V. Parker 757* (JEPS) and *V. Parker 759* (JEPS), at a site southwest of Dubakella Mountain, Trinity Co., California].

In summary, members of the ultramafic clade of *Harmonia* appear to be outstanding examples of serpentine neoendemics, that is, groups that evolved on ultramafics, rather than relicts or paleoendemic taxa secondarily restricted to serpentines (see Stebbins 1942; Kruckeberg 1954, 1984; Stebbins and Major 1965; Raven and Axelrod 1978; Mayer and Soltis 1994a, b).

*Rarity.* Discovery of *H. guggolziorum* along a paved, public road less than 3 miles from US Highway 101 at Hopland, near a University of California field station, probably reflects extreme rarity of the species and insufficient access by botanists to serpentines in the vicinity. Smith and Wheeler (1990–1991) explored some nearby ultramafic sites in Mendocino County and did not report any species referable to *Harmonia* in their flora of Mendocino County. I did not find collections of *H. guggolziorum* at CAS, CHSC, DAV, JEPS, PUA, ROPA, UC, or the herbarium of the University of California Hopland Research and Extension Center and am unaware of any collections of the species from anywhere other than the holotype and paratype localities. *Harmonia guggolziorum* is probably naturally rare, based on the paucity of documented localities for other serpentine harmonias; *H. doris-nilesiae, H. hallii,* and *H. stebbinsii* are all listed as rare or endangered (List 1B) by the California Native Plant Society (2001). Exploration for new populations of *H. guggolziorum* on ultramafics of southern Mendocino County and adjacent counties is needed.

I am pleased to name this species for Jack and Betty Guggolz of Cloverdale, California, who collected the first specimens of *Harmonia guggolziorum* and who have contributed significantly to conservation of California's North Coast Range flora through years of dedicated effort.

## Acknowledgments

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